

DEFOLIATION RESPONSE AND GROWTH OF  
*NASSELLA PULCHRA* (A. HITCHC.) BARKWORTH FROM  
SERPENTINE AND NON-SERPENTINE POPULATIONS

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ABSTRACT

Restoration of stands of the native bunchgrass *Nassella pulchra* (A. Hitchc.) Barkworth in the California grassland requires suitable germplasm and conditions favoring survival, reproduction, and recruitment. In a common garden experiment, growth patterns of two populations of *Nassella pulchra* were compared. Because defoliation by herbivory and burning are ubiquitous influences on the California grassland, and have been suggested as having potential for manipulating the balance of native and non-native species, the response of each population to clipping in winter, winter and early spring, and late spring was also compared. The two populations exhibited genotypic variation in morphology, growth, and response to clipping. Clipping in winter had no significant effect on tiller number, number of inflorescences, or leaf length. Clipping in winter and early spring significantly reduced number of tillers and inflorescences in plants from one population, grown from seed collected on a serpentine site, but not from the non-serpentine population. Clipping in late spring severely reduced tiller numbers, number of inflorescences, and leaf length in plants from both sites. The need for use of local seed sources for restoration is well-recognized, but the characteristics of seed source site, as related to genetic characteristics, may also affect the success or failure of restoration efforts and management practices. In the populations studied, a perennial grassland restoration system using winter burning and/or grazing to influence annual grasses would not damage *N. pulchra* plants, but response to early spring treatments and frequency or duration of treatment varies by population.

The displacement of California's once extensive native prairie by introduced annual grass species began in the late 18th century following introduction of livestock and exotic plants (Heady et al. 1991), possibly augmented by changes in fire frequency brought about by Euro-American settlement. Native grasses now are uncommon, found mostly as relict stands within a few km of the Pacific

Ocean and farther inland on serpentine soils (Murphy and Ehrlich 1989). Recent increased interest in grassland conservation and restoration (Hatch et al. 1991) follows a long history of poor success at propagating native grasses (Kay et al. 1981). The success of native grassland conservation and restoration projects will in large part depend on development of propagation and management techniques informed by knowledge of potential species distribution, genetic variability of populations, and response to management techniques for maintaining and encouraging native species.

Found on a variety of sites, the widely distributed perennial bunchgrass *Nassella pulchra* is considered to be the former dominant of the Valley Grassland portion of the native prairie (Heady 1977) and is the most common native perennial in the grassland today (Bartolome and Gemmill 1981). The species is widely considered a primary candidate for use in restoring native grassland. Native grassland restoration projects in California are primarily geared towards seeding, transplanting, or increasing native perennial stands. Herbivory and fire are major ecological influences on the California grassland. It is likely that restoration and maintenance of native grasses will include some grazing (Murphy and Ehrlich 1989) or burning, but information on their effects on restoration outcomes is limited and sometimes seemingly contradictory, perhaps due to variation in restoration site conditions or the genetic characteristics of *Nassella pulchra*.

Early research by range ecologists investigated the effects of defoliation on native perennials including *Nassella pulchra* (Sampson and McCarty 1930; Parker and Sampson 1931) and the potential for native perennial-based range improvement (Jones and Love 1945; Kay et al. 1981). *N. pulchra* was found to be intolerant of grazing during spring (Parker and Sampson 1931), and subsequent recommendations for range improvement emphasized available non-native perennials, not natives (Love 1951). More recent research has gone beyond this cursory knowledge of the dynamics of the species, showing that *Nassella pulchra* is favored by fire (Hatch et al. 1991), and does not necessarily recover (Heady et al. 1991) or may even disappear with grazing removal (Bartolome and Gemmill 1981). A number of exotic annuals aggressively increase under conditions of light or no grazing and have been observed to exclude natives including *Nassella pulchra* (Bartolome and Gemmill 1981). Effective maintenance of *N. pulchra* in restored grasslands will depend upon selectively suppressing the aggressively competitive annuals without damage to perennials (Dennis 1989).

One proposed scheme to encourage *N. pulchra* uses late fall burning to kill germinated annuals and winter grazing to further reduce annual grass competition (Hatch et al. 1991). If this is to work, it also must not significantly damage *N. pulchra* plants. Dennis (1989)

found that *Nassella pulchra* was more tolerant than other native grasses to defoliation during winter and early spring. However, burning and grazing can result in reduced tiller numbers, reduced reproductive output, and reduced plant vigor, as occurred in one experiment in which these treatments were applied in summer (Langstroth 1991). All of this research has been done *in situ* in the California prairie, where the influence of annual species may make it difficult to evaluate the influence of defoliation on *Nassella pulchra* independent of environmental modification by annual species (Dennis 1989). In addition, nothing is known about the population genetics of *Nassella pulchra*, and how genetic variability may affect response to management. This study addresses both of these concerns.

In order to explore genetic variation in the species, a common garden experiment was carried out to compare growth patterns and response to management of *Nassella pulchra* from seed gathered from two distinct Bay Area populations. Because defoliation by herbivory and burning are ubiquitous influences on the California grassland, and have been suggested as having potential for manipulating the balance of native and non-native species, the response of each population to clipping in winter, winter and early spring, and late spring was also compared in controlled conditions. Tiller number, number and status of culms, and leaf length were used as measures of plant vigor and reproductive output.

#### METHODS

Approximately 500 seeds from randomly selected individuals of *Nassella pulchra* were collected at two sites along the shore of San Francisco Bay. The Ring Mountain site in Marin County, California, is on a serpentine soil similar to the Montara series (P. Zinke personal communication), tentatively identified as Henneke Stony Clay Loam (USDA, SCS 1985). Ring Mountain had not been grazed by livestock for 20 years prior to the study, but has previously supported large numbers of cattle. The other site was 10 km away at Point Molate, in Contra Costa County, on a non-serpentine soil, Los Gatos Clay (Welch 1977). Point Molate has been ungrazed by livestock since approximately 1940 (Havlik 1984). The vegetation at both sites was dominated by *N. pulchra* in association with other typical Bay Area coastal prairie species (Heady et al. 1977). Seeds were germinated in fall (germination rate was 80 percent) and seedlings grown in a greenhouse in a flat.

Phenology, growth, and clipping studies were conducted in specially constructed planter boxes located in Strawberry Canyon on the University of California, Berkeley Campus. The boxes were 4 × 8 × 2 feet on a slightly sloping concrete slab and filled with a Dibble Clay Loam Soil (Welch 1977), a commonly available garden

soil. A randomly selected group of three-month-old seedlings, 20 from the Point Molate non-serpentine population, and 20 from the Ring Mountain serpentine population plants, were transplanted from the greenhouse to the planter boxes in Strawberry Canyon. Plants were randomly located in a grid with 20 cm spacing. Plants grew under conditions normal for the San Francisco Bay Area in winter and early spring, with adequate soil moisture from rainfall until early May. Plots were kept free of other species during the experiment.

Twenty year-old plants from each population were randomly assigned to be clipped to a 5 cm stubble height in three different treatments plus unclipped controls: 1) Clipped in early winter only (December 8,  $n = 10$ ), 2) Clipped in early winter and early spring (December 8 and March 11,  $n = 10$ ), 3) Clipped in mid-spring (May 10,  $n = 10$ , and 4) unclipped ( $n = 10$ ). Plant response was measured as total number of tillers/plant, number of flowering culms per plant, and length of leaf (blade + sheath) recorded from the longest leaf on six permanently tagged tillers measured per plant. Plants were measured on January 13 (mid-winter), March 11 (early spring), April 21 (mid-spring), and June 9 (late spring).

Results were analyzed by two-way ANOVA for significant response by population (Ring Mountain or Point Molate) and clipping treatment on the last measuring date (June 9), followed by mean separation using least significant differences. The last sample date was chosen for comparison because plants in the California prairie senesce in early summer or late spring. This date therefore takes into account all of the potential rain-year growth or re-growth. Differences in growth pattern between populations for the control plants were analyzed using separate one-way ANOVAs for each sample date. We rejected the null hypotheses of no significant treatment or population effect at  $\alpha = 0.10$ . The significance level was selected to balance power of the test against the low "risk" associated with Type I error.

## RESULTS

There were differences in the growth patterns and morphological characteristics of plants from the two populations that were obvious visually and borne out by measurement. Plants from Point Molate appeared coarser than the finer textured plants from Ring Mountain, and matured faster. *Nassella pulchra* plants from Ring Mountain averaged more tillers per plant than those from Point Molate (Fig. 1). On the other hand, Point Molate plants grew earlier or faster, producing more inflorescences on the early spring sample date than the plants from Ring Mountain (Fig. 2), and losing tillers by June as they began to senesce (Fig. 1). Point Molate plants also had longer leaves at each sample date (Fig. 3).

The two populations also varied in their response to treatment.

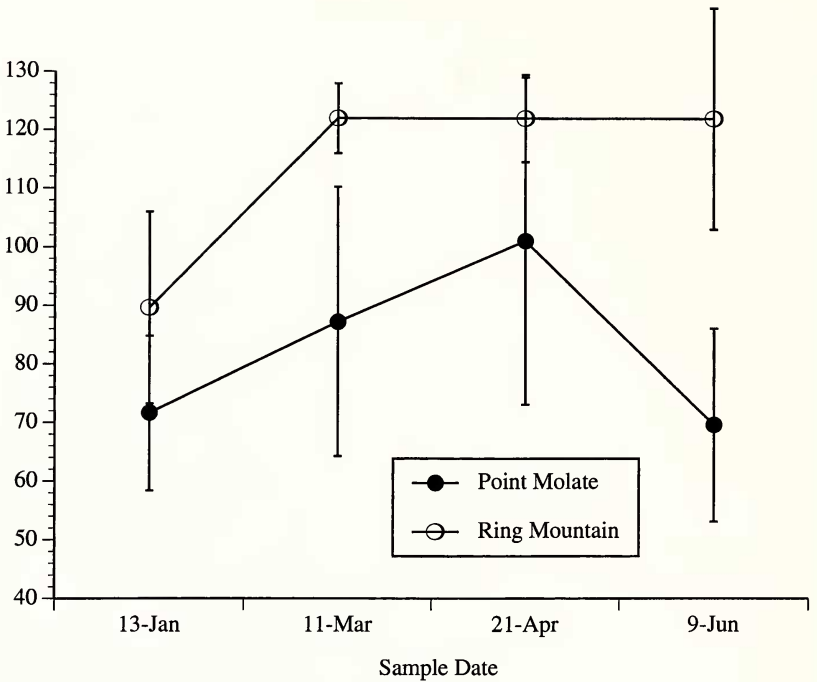


FIG. 1. Number of tillers per unclipped plant by sample date for plants from two populations, Ring Mountain serpentine and Point Molate non-serpentine.  $n = 5$  for each data point. Only the difference between populations on June 9 is significant ( $P < 0.1$ ).

Number of tillers per plant on June 9 differed significantly between populations and among clipping treatments (Fig. 4). Plants from Ring Mountain averaged  $98 (\pm 11)$  tillers and plants from non-serpentine populations at Point Molate averaged  $47 (\pm 6.5)$  tillers, a difference significant at  $P < 0.001$ . Plants clipped to a 5 cm stubble height on December 10 did not differ significantly from controls in number of tillers, but Point Molate plants clipped twice, in December and March, and plants from both populations clipped once in spring, on May 10, had significantly fewer tillers than controls ( $P < 0.01$ ).

Number of inflorescences was significantly affected by clipping date ( $P < 0.01$ ), with no effect from the single December clipping, significantly fewer inflorescences from the December plus March clipping in Ring Mountain plants, and markedly fewer inflorescences on both populations with the May clipping (Fig. 5).

Length of the longest leaf was significantly affected by clipping treatment ( $P < 0.01$ ). December clipping did not show a significant

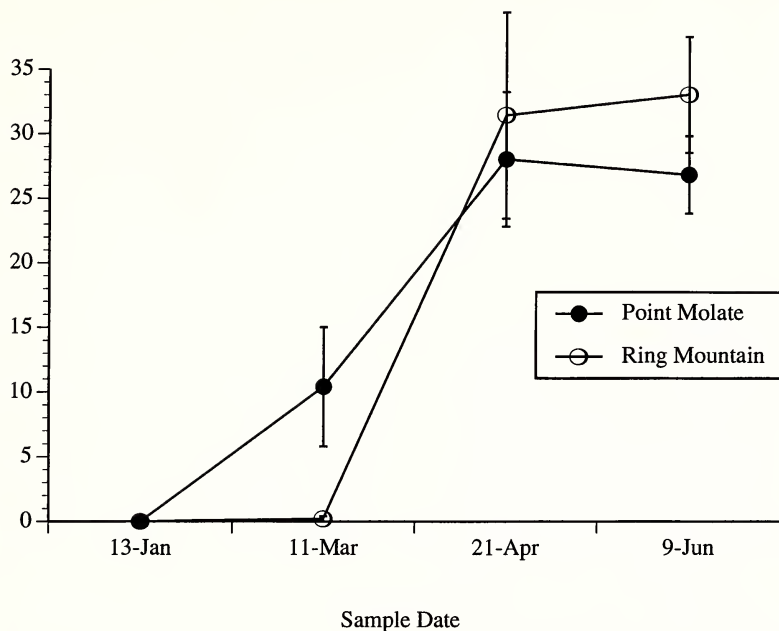


FIG. 2. Number of inflorescences per unclipped plant from two populations, Ring Mountain serpentine and Point Molate non-serpentine.  $n = 5$  for each data point. Only the difference between populations on March 11 is significant ( $P < 0.1$ ).

effect, but both populations produced shorter leaves after the December plus March and May treatments (Fig. 6).

#### DISCUSSION

The two populations differed significantly in their patterns of growth and in response to clipping when grown in common on the same soil. Plants from Ring Mountain produced more tillers per plant. Plants from Pt. Molate flowered earlier, produced longer leaves, and senesced earlier than plants from Ring Mountain.

When compared to controls, *Nassella pulchra* plants from both sites were little affected by December clipping, with no significant changes in number of tillers, number of inflorescences, and leaf length. When a second clipping was added to the December clipping, the plants from the two populations responded differently. Ring Mountain plants had a significant reduction in number of inflorescences and tillers, while Point Molate plants were no different from controls. This result is surprising because it contradicts the hypothesis of Parker and Sampson (1931), that the time of culm elevation is when grasses are most susceptible to losses in productivity due to defoliation. The Point Molate plants had more elevated culms at the March clipping date

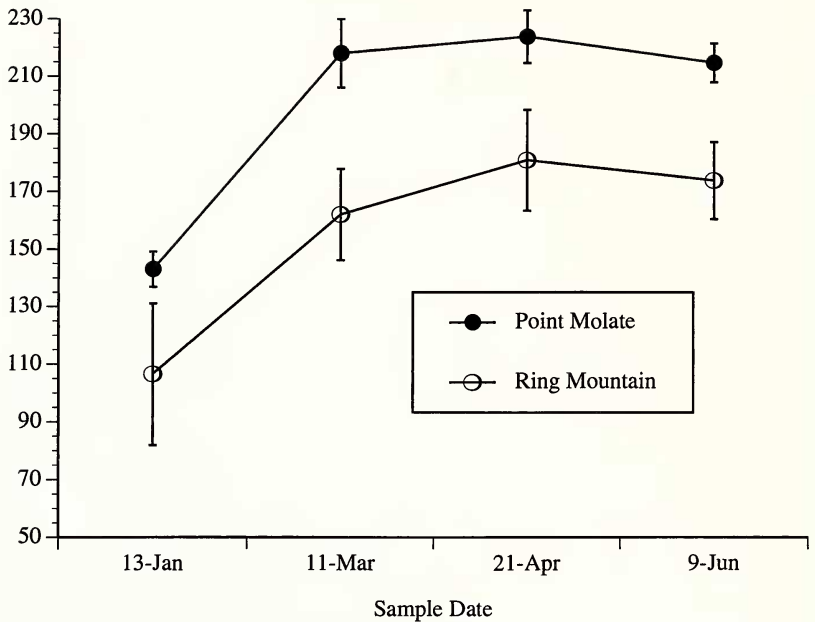


FIG. 3. Length of longest leaf for unclipped plants from two populations, Ring Mountain serpentine and Point Molate non-serpentine. The length is length of blade plus sheath for the longest leaf on six marked tillers on each plant. All differences between populations are significant except June 9 ( $P < 0.05$ ).

than the Ring Mountain plants. Both populations had a shorter leaf length as a result of the double clipping, perhaps because regrowth of leaves was limited in late spring, while investment in tillers and inflorescences continued in the Point Molate plants. All plants, as predicted by previous work, were severely affected by May clipping, probably because they had only 4 weeks to recover before the June measurement and senescence.

The Ring Mountain plants were gathered from a serpentine site, while the Point Molate plants were from a non-serpentine associated population. In California today, most noticeable stands of *Nassella pulchra* and other native perennials are associated with serpentine soils, where competition from native annuals is reduced. It can be hypothesized that the growth patterns of the plants from the non-serpentine site reflect adaptation to a denser grassland, crowded with introduced plants. Earlier or more rapid growth and flowering, and larger leaves, may be important in competing with fast growing annuals. As with all greenhouse or lab experiments, it is also possible that response to treatment and growth characteristics may be influenced by environmental characteristics when the plants are in

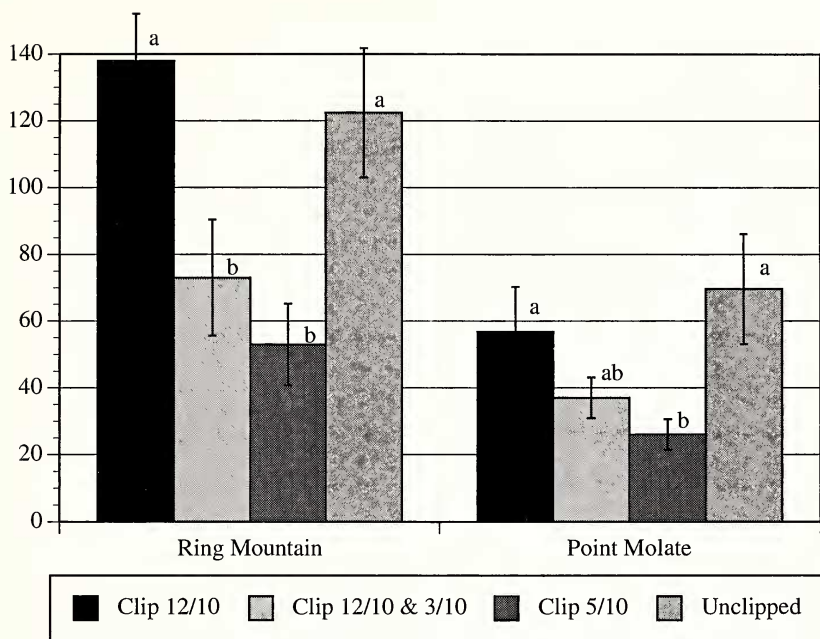


FIG. 4. Effect of clipping on number of tillers per plant on June 9 for two populations. Means for bars within populations sharing letters are not significantly different (LSD,  $P < 0.05$ ).

the field. This study has controlled environmental factors in order to examine genetically-determined differences in population behaviors. Genetic variation in *Nassella pulchra* may help explain the varying results of restoration efforts and research.

As relic areas for native species are often found on serpentine sites, seed for restoration of both serpentine and non-serpentine sites is often collected from them. This study shows that matching the site characteristics of seed source and planting site, or at least using a mix of seed sources, may be just as important a consideration as simply looking for a "local" seed source. Re-vegetating non-serpentine sites with seed from serpentine-adapted populations may put the new plants at a disadvantage when the major constraints to growth are competitive rather than soil characteristics. Conversely, plants from non-serpentine sites might not flourish when soil nutrient regimes fail to support their genetically programmed growth pattern. Obviously, these hypotheses, while suggested by this research, require testing with broad replication using germplasm from a variety of serpentine and non-serpentine sites.

These results of treatment of these populations, corroborated by the research of Dennis (1989), indicate that winter grazing, mowing,



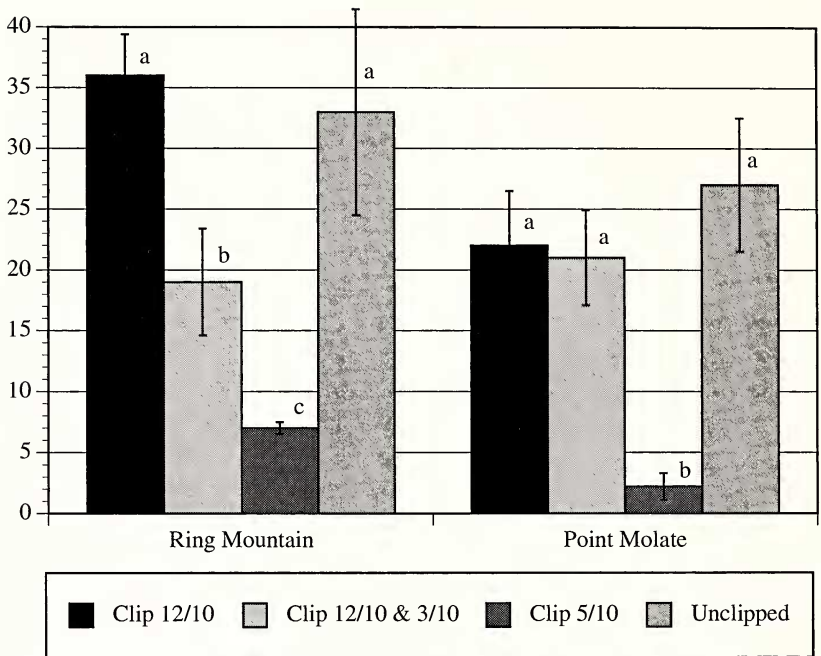


FIG. 5. Effect of clipping on number of inflorescences per plant on June 9 for two populations. Means for bars within populations sharing letters are not significantly different (LSD,  $P < 0.05$ ).

or low-intensity burning of *Nassella pulchra* is unlikely to affect plant vigor or reproductive output. Management regimes designed to reduce competing annuals by concentrating defoliation in fall and winter show promise for the restoration and maintenance of *N. pulchra* stands. It also appears that timing of the removal of grazing or further defoliation in spring will be important and may differ for different *N. pulchra* populations. For Ring Mountain serpentine plants, the additional defoliation on March 10 significantly reduced the number of tillers and inflorescences at the end of the season compared to controls, while the number of inflorescences and tillers produced by Point Molate non-serpentine plants was not significantly affected.

Management systems using fall or winter burning and/or grazing to reduce competition from annual grasses are based on the premise that reduction of annual plant biomass and/or density allows perennials opportunity for better seedling survival and seed output. This should allow for increase of *Nassella* plant density and offer potential for grassland rehabilitation. However it is important to note that *N. pulchra* populations may respond differently to defoliation, and

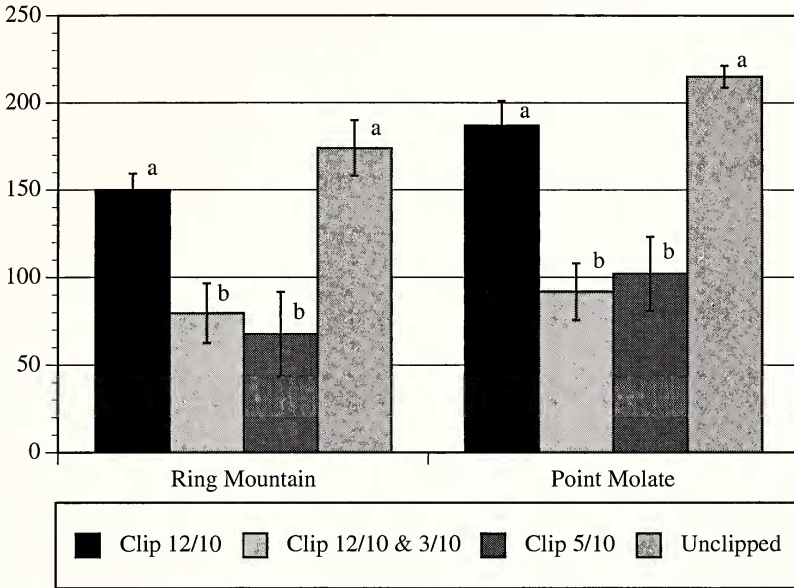


FIG. 6. Effect of clipping on length of longest leaf on June 9 for two populations. The length is length of blade plus sheath for the longest leaf on six marked tillers on each plant. Means for bars within populations sharing letters are not significantly different (LSD,  $P < 0.05$ ).

that other native perennial grasses are affected very differently by defoliation and competition with exotic annuals (Dennis 1989).

Most of the evidence that *Nassella pulchra* or any other perennial bunchgrass once dominated the now annual Valley Grassland is inferred from supposed relict stands of native perennials and poorly tested successional models that suggest trends toward perennial grass dominance (Heady et al. 1992). One study using opal phytoliths produced the only direct evidence for former perennial grass dominance on a now annual site in the Valley Grassland (Bartolome et al. 1986). Heavy year-long grazing by livestock is usually considered to have weakened and killed the native grasses, allowing for the rapid colonization of annuals from the Mediterranean (Burcham 1957; Baker 1989). Yet direct evidence that livestock grazing eliminated the perennial grasses is lacking, suggesting that the simple introduction of Mediterranean annuals may have been enough to quickly eliminate native plants (Bartolome 1989) on sites where site factors such as serpentine soils do not inhibit the growth of the exotics. For these reasons, consideration of site specific population-level adaptations to serpentine vs. non-serpentine growing conditions, and to management regimes designed to maintain stands by reducing competition from exotics, should be an important consid-

eration in seed-source collection for restoration projects. Most restoration efforts today are necessarily on non-serpentine sites—perhaps the seed collected for these efforts should also come from non-serpentine sites, or from a variety of sites or populations, a challenge given the fact that the most extensive stands remaining are generally on serpentine areas.

## LITERATURE CITED

- BAKER, H. G. 1989. Sources of the naturalized grasses and herbs in California. Pp. 29–38 in L. F. Huenneke and H. Mooney (eds.), *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Dordrecht.
- BARTOLOME, J. W. 1989. Ecological history of the California Mediterranean-type landscape. Pp. 2–15 in W. J. Clawson (ed.), *Landscape ecology: study of Mediterranean grazed ecosystems*. Proceedings MAB Symposium, XVI Int. Grassland Congress, Nice, France, Oct 7, 1989.
- BARTOLOME, J. W. and B. GEMMILL. 1981. Ecological status of *Stipa pulchra* (Poaceae) in California. *Madroño* 28:172–184.
- BARTOLOME, J. W., S. E. KLUKKERT, and W. J. BARRY. 1986. Opal phytoliths as evidence for displacement of native Californian grassland. *Madroño* 33:217–222.
- BURCHAM, L. T. 1957. California rangeland. California Division of Forestry, Sacramento.
- DENNIS, A. 1989. Effects of defoliation on three native perennial grasses in the California annual grassland. Ph.D. dissertation. University of California, Berkeley. 144 p.
- HATCH, D., J. W. BARTOLOME, and D. HILLYARD. 1991. Testing a management strategy for restoration of California's native grasslands. Pp. 343–349 in *Proceedings of the Symposium on Natural Areas and Yosemite: prospects for the future*.
- HAVLIK, N. A. 1984. Effects of urban-industrial land use on vegetation and flora in the Potrero Hills, California. Ph.D. dissertation. University of California. 141 p.
- HEADY, H. F. 1977. Valley grassland. Pp. 491–519 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. Wiley, NY.
- HEADY, H. F., J. W. BARTOLOME, M. D. PITT, M. G. STROUD, and G. D. SABELLE. 1991. California grassland. Pp. 313–335 in R. T. Coupland (ed.), *Natural grasslands, ecosystems of the world*, Vol. 8A. Elsevier Scientific Publishing Company, Amsterdam.
- JONES, B. J. and R. M. LOVE. 1945. Improving California ranges. California Agricultural Extension Service Circular 129.
- KAY, B. L., R. M. LOVE, and R. D. SLAYBACK. 1981. Discussion: revegetation with native grasses: I. A. disappointing history. *Fremontia* 9:11–15.
- LANGSTROTH, R. P. 1991. Fire and grazing ecology of *Stipa pulchra* grassland: a field study at Jepson Prairie, California. M.S. thesis. University of California, Davis. 75 p.
- LOVE, R. M. 1951. Range grass and reseeding experiments in California. *Calif. Agric.* 5:8–10.
- MURPHY, D. D. and P. R. EHRlich. 1989. Conservation biology of California's remnant native grasslands. Pp. 201–211 in L. F. Huenneke and H. Mooney (eds.), *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Dordrecht.
- PARKER, K. W. and A. W. SAMPSON. 1931. Growth and yield of certain gramineae as influenced by reduction of photosynthetic tissue. *Hilgardia* 5:361–381.
- SAMPSON, A. W. and E. C. MCCARTY. 1930. The carbohydrate metabolism of *Stipa pulchra*. *Hilgardia* 5:61–100.
- U.S. DEPARTMENT OF AGRICULTURE, SOIL CONSERVATION SERVICE. 1985. Soil survey

of Marin County, California. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C.

WELCH, L. E. 1977. Soil survey of Contra Costa County, California. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C.

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## NOTEWORTHY COLLECTIONS

### COLORADO

*POLEMONIUM CONFERTUM* A. Gray (POLEMONIACEAE).—Gunnison Co., Gunnison National Forest, 45.0 km N and 14.5 km E of Gunnison, in tundra and fellfield on summit of North Italian Mountain, T13S R84W S2, 38°55'N, 106°45'W, 4027 m, 19 July 1994, *R. Seagrist 569* (RMBL); Park Co., Buffalo Peaks Wilderness Area, Pike National Forest, 17.7 km N of Buena Vista, common along boulder-lined snow-melt streams on tundra-covered plateau 3.2 km NE of East Buffalo Peak summit, T12S R78W S22, 39°0'30"N, 106°5'W, 3780 m, 22 July 1995, *R. Seagrist 1008* and *K. Taylor 140* (RMBL, MO); Gunnison Co., Maroon Bells-Snowmass Wilderness Area, White River National Forest, 22.5 km N and 4.0 km W of Crested Butte, intermittent in tundra and fellfield along dividing ridge between Hasley Basin and Fravert Basin, T11S R86W S30, 39°3'30"N, 107°2'W, 3856 m, 3 August 1995, *R. Seagrist 1133* (RMBL); Gunnison Co., Maroon Bells-Snowmass Wilderness Area, White River National Forest, 20.9 km N and 2.4 km W of Crested Butte, intermittent in tundra and fellfield at Frigid Air Pass, T11S R86W S32, 39°3'N, 107°1'30"W, 3780 m, 13 August 1995, personal observation by R. Seagrist and K. Taylor; Gunnison Co., Maroon Bells-Snowmass Wilderness Area, White River National Forest, 22.5 km N of Crested Butte, in tundra and fellfield on Maroon Peak, T11S R86W S27, 39°4'3"N, 106°59'W, 3659 to 4316 m, 13 August 1995, personal observation by K. Taylor.

*Previous knowledge.* This species was first collected by Hall and Harbour (450) in 1862 from Jefferson Pass in Colorado's Mosquito Range and first described by Gray in 1864 (A. Gray, *Proceedings of the Academy of Natural Sciences, Philadelphia* 1863:73). Although some authorities regard *Polemonium confertum* as a variety of *P. viscosum* Nuttall, it is sufficiently distinct in several characters that it is considered to be a separate species by Brand (*Das Pflanzenreich* 250:44, 1907), Rydberg (*Flora of the Rocky Mountains and Adjacent Plains* 2nd ed., New York Botanical Garden, 1922), Wherry (*American Midland Naturalist* 27:741–760, 1942), Grant (*Botanical Gazette* 150(2):158–169, 1989), and Weber (*Colorado Flora: Eastern Slope*, Colorado Assoc. University Press, Boulder, 1990). Our field and herbarium observations agree with the above authorities that *P. confertum* is quite distinct. Our specimens have characteristics which meet the description of *P. confertum* provided by Grant (1989), including widely-spaced whorled leaflets, orange anthers, light blue corollas broadly funnelliform in shape with throats wider than 10 mm, and inflorescences 40–50 mm wide.

*Significance.* Our collections are the first from the Maroon Bells-Snowmass and Buffalo Peaks regions and extend the known range of this species considerably. Previously thought to be fairly rare, it appears that *P. confertum* is actually fairly common but grows in high elevation, hard-to-access habitats.

—RANDY V. SEAGRIST and KEVIN J. TAYLOR, Rocky Mountain Biological Laboratory, Crested Butte, CO, 81224.